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Intra-annual variation and landscape composition interactively affect aphid community composition

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Abstract. Agricultural intensification impacts local arthropod communities. The temporal and spatial variation of agricultural environments can have a significant impact on insect pest populations, yet little work has been done to date on the effect of intra-annual variation (within season) or spatiotemporal effects on arthropod functional community composition. The aim of this research was to evaluate the effects of intra-annual variation and landscape composition on the aphid community. To that end, we investigated the following research question: How do intra-annual variation and landscape composition affect aphid abundance, species richness, and functional community composition? In this study, we quantified landscape composition as percent cropland, intra-annual variation as sampling week measured throughout the growing season, and aphid functional community composition as crop virus transmission—or vectoring—ability. We collected data in two agricultural regions: a diversified agricultural region in New York State (NY) and an agriculturally intense potato-growing region in Wisconsin (WI). We found that the interactive effect of landscape composition and intra-annual variation significantly affected aphid abundance and species richness in both study regions, and functional community composition in NY. These results indicate that spatiotemporal shifts in agroecosystems have significant implications for aphid functional community composition.

Key words: agroecology; insect-vectored pathogen; landscape epidemiology; vector ecology.

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INTRODUCTION

The effect of landscape composition on local communities often varies over time, with temporal shifts and landscape structure interactively shaping local communities. Tscharntke et al. (2012) describe this phenomenon in their landscape-moderated concentration and dilution hypothesis, which posits "spatial and temporal changes in landscape composition can cause transient concentration or dilution of populations with functional consequences." Most research in this area has explored the effect of inter-annual variation in landscape composition (e.g., habitat fragmentation) on local species richness or the abundance of particular species (Debinski and Holt 2000). These studies show a wide range of species-specific responses to landscape modification and demonstrate that transient effects dominate in many systems (Debinski and Holt 2000, Grez et al. 2004). Inter-annual habitat modification (e.g., cropping sequences) not only results in the transient concentration and dilution of species (Thies et al. 2008), but can also impact species

interactions (Tylianakis et al. 2007). Both effects could impact the functional composition of the community, and similar effects could occur within a growing season. Yet to date, little work has been done on intra-annual (within season) shifts or their impact on the functional composition of local communities (Tscharntke et al. 2012), despite their possible implications for agricultural pest pressure and vector-borne crop disease spread. In this study, we compare data from two potato-producing areas to explore the interactive effects of landscape composition and intra-annual variation on local insect pest abundance, species richness, and functional community composition.

This work is informed by our previous research, which demonstrated a direct relationship between the percentage of cropland in the surrounding landscape and end-of-season Potato virus Y (PVY, a non-persistent aphid-borne crop virus) prevalence on small-scale farms in New York State (Claflin et al. 2016). Greater percentages of cropland within radiuses ranging from 500 m to 1500 m had significantly higher PVY prevalence, and this relationship appeared to be mediated by the direct effect of the landscape on the aphid community. In this study, we delve deeper into the data we collected in New York State, as well as data collected in Wisconsin, to further develop our understanding of the relationship between landscape composition and the aphid vectors of PVY, with particular emphasis on spatiotemporal and functional trait effects.

Spatiotemporal effects are likely inherent in this system, because agricultural systems are fragmented both spatially and temporally and are subject to high levels of disturbance and variation. Because landscape composition in the surrounding area affects the connectivity and permeability of the landscape for agricultural pests (Margosian et al. 2009), these shifts can affect the abundance and composition of the local arthropod assemblage. Shifts in landscape composition over time associated with agricultural intensification, such as habitat loss and fragmentation, increased chemical inputs, and increased crop cover, can affect insect pest abundance, and these effects are often species-specific (Banks 1998, Braschler et al. 2003, Weibull and Östman 2003, Grez et al. 2008, O'Rourke et al. 2011, Zhao et al. 2015). Land use, vegetation type, and management style have also been found to affect the composition of arthropod assemblages in groups ranging from bees to spiders (Rusch et al. 2014, Torma et al. 2014, Woodcock et al. 2014). For example, Woodcock et al. (2014) found that the amount of arable crop production and semi-natural habitat cover had opposing effects on the functional diversity of ground beetles and bees. The arable crop production was negatively correlated with functional diversity, while the semi-natural habitat cover was positively correlated with functional redundancy.

Temporal shifts, such as seasonal variation in weather, precipitation, and environmental disturbance, such as raking, desiccation, or other management practices, can affect insect pest abundance and movement (Cocu et al. 2005, Narayandas and Alyokhin 2006, Krauss et al. 2011, Davis et al. 2014). Cardinale et al. (2006) found that the asynchronous mowing of alfalfa fields caused a difference of several orders of magnitude in pea aphid (*Acyrthosiphon pisum* Harris) density among alfalfa fields, resulting in significant spatial and temporal variation. Seasonal insect pest movement is not random; Vialatte et al. (2006) found that aphids have preferred routes and that most of the aphids colonizing wheat came from another crop, maize. By changing the proportion of each species in the insect pest assemblage, seasonal shifts in species abundances could alter the species composition, and possibly the functional composition of the community.

The diverse community of aphid vectors suggests that functional community composition may also play an important role in the PVY pathosystem. A large suite of aphid species vector PVY. Aphid vector species vary widely in transmission efficiency (the probability of virus transmission from an infected to an uninfected host plant) and life history (Gray et al. 2010). Many aphid vector species are non-colonists (do not settle and reproduce) on potato. Although the most efficient PVY vector, the green peach aphid (*Myzus persicae* Sulz.), is a potato-colonizing species (i.e., settles and reproduces on potato), the large vector assemblage is mostly comprised of non-colonists (Gray et al. 2010).

In this study, we explored two important functional attributes in the aphid community with respect to PVY risk: (1) the proportion of aphids that were known PVY vectors and non-vectors,

and (2) the proportion of aphids that were undefined PVY vector species (with no published transmission efficiency), and the proportion with low and high transmission efficiencies. In this context, altering the aphid functional community composition could have significant implications for predicting pest pressure and PVY risk.

The aim of this study was to evaluate the effects of intra-annual variation and landscape composition on the aphid community. To explore this, we investigated the following sequential research predictions: (1) Spatiotemporal effects, as measured in the interactive effect of landscape composition and intra-annual variation, will have a significant impact on the aphid community; (2) as predicted by the *landscape-moderated concentration and dilution hypothesis*, those spatiotemporal effects will impact aphid functional community composition; and (3) based on our previous findings linking landscape composition and PVY prevalence, we predict that sites surrounded by greater amounts of cropland will have higher proportions of efficient PVY vectors in the aphid community throughout the season. To address these predictions and assess the consistency of our results, we evaluated two study regions. We analyzed data collected in two 2-yr surveys of the aphid community in potato fields: one in an agriculturally intense region in central Wisconsin (WI) in 2010 and 2011 and the other in the diversified Finger Lakes region of New York State (NY) in 2012 and 2013.

Methods

Study system

Aphids are a major crop pest and cause significant crop damage, both directly through phloem feeding and indirectly by vectoring crop pathogens (Dedryver et al. 2010). Because plants infected with PVY are difficult to identify and rogue (remove) in the field, and PVY has a very rapid period of inoculation (e.g., within seconds of initial probing behavior), effective mitigation strategies are limited, and insecticide use offers little advantage (Gray et al. 2010). There is also an unusually large (>40 species) suite of known vector species. These characteristics make the aphid community tractable for exploring questions about functional community composition and abundance, with respect to PVY spread.

Farm sites

In NY, sampling took place at 19 farms in 2012 and 21 farms in 2013 (including 17 of those sampled in 2012). The farms were located throughout the Finger Lakes region and grew multiple cultivars of potatoes. Field management practices varied between the farms. However, all but three farms used little to no pesticides. The sites constituted a gradient of landscape composition, ranging from 3.6% cropland within 500 m to 92.3% cropland within 500 m (Appendix S1: Table S1).

In WI, sampling took place at 9 sites in 2010 and 9 sites in 2011. One 2010 site was excluded from analyses because there was significant overlap in the surrounding landscape (i.e., it was too near) with other sites. The sites constituted a gradient of landscape composition, ranging from 41.5% cropland within 500 m to 95.6% (Appendix S1: Table S1).

Land use within 500 m of the site was calculated using the 2010, 2011, 2012, and 2013 Cropland Data Layers (USDA National Agricultural Statistics Service, Cropland Data Layer), respectively, and ArcGIS software (ArcMap 10.2; ESRI, Redlands, California, USA) and was divided into three categories: cropland, unmanaged land, and other. The data layer is a remotely sensed, categorical description of crop and semi-natural land using georeferenced 30 × 30 m squares (raster pixels) that can be used to measure spatial patterns of crop production. Detailed accuracy assessment estimates are published for individual crops in both NY and WI, and the large area row crops have accuracies ranging between 85% and 95% accuracy. All managed land, including pasture, was included as cropland. Fallow or idle cropland and forested land categories were included as unmanaged land. Developed land, barren land, and open water were categorized as other. The sites were at least 1 km apart. Mantel tests were used to test for spatial autocorrelation of landscape simplification. The results for the Mantel tests were not significant (Appendix S1: Table S2), indicating that our measure of landscape simplification was not spatially autocorrelated.

Sampling schedule

In NY, the sites were divided into two groups, based on their distance from Ithaca: those sampled weekly (11 farms in 2012 and 12 in 2013), and those sampled periodically (2–3 times)

during the growing season (8 farms in 2012 and 9 in 2013). For the sites sampled each week, the insect traps (see below) were collected and replaced at each visit. The traps were collected and removed after a week at the sites sampled periodically. In WI, all sites were sampled weekly through the sampling interval.

Sampling insect abundance and community composition

To sample the aphid community in NY, nine pan traps were placed at each farm approximately 3–4 weeks after planting, when plants were emerging, with three traps in each of three rows. The traps were placed in the two peripheral rows and the center row of each site. The pan traps were made in the style of green tile traps: a hard 17.5 × 16 × 9 cm plastic box with green plastic that mimics the reflectance of leaves (4430 Filter; Rosco, Markham, Ontario, Canada) glued to the bottom of the pan. Each trap was filled with water containing two drops of dish soap to lessen the surface tension of the water into which alate aphids would drop and not escape. Traps were suspended approximately 1 m off the ground on a rebar stake (Boiteau 1990). The traps were placed approximately midway down the length of a potato row, with 2 m between traps.

In WI, sampling was conducted in a similar manner, except that the pan traps contained a green tile—instead of plastic material—to mimic the surrounding plants. They also contained a mixture of 50:50 propylene glycol: water, instead of a water–soap mixture. Twenty-one traps were set at each site along four transects of five traps per transect at each sampling location. Each transect was aligned in each cardinal direction with traps positioned at 3.05 m outside the potato field in the weedy margin, at the field edge (0 m), between the weedy margin and potatoes, 3.05 m into the potato field, 7.62 m into the potato field, and 15.24 m into the potato field. The final trap was positioned as close to the center of the field as possible. Trap positioning within the row and above the canopy was similar to NY and was adjusted weekly to remain just above the developing potato canopy.

Each trap was collected and replaced after one week. The water traps were sieved using a 1 mm^2 mesh screen, and the collected specimens were stored at room temperature in 70% ethanol for later identification. Following collection, aphids were identified to species using morphological characters (Pike et al. 2003, key; D. Voegtlin and D. Lagos, *personal communication*). In NY, 72% (1240) of aphid specimens were identified to species, 21% (366) were identified to genus, and the remaining 7% (113) could not be resolved. Aphid abundance was calculated as a surrogate term for magnitude of capture, by dividing the total number of aphids collected at a site by the number of water traps. In WI, 79% (3604) of the aphid specimens were identified to species, 18% (809) were identified to genus, and the remaining 3% (130) could not be resolved. Aphid species richness was calculated as the number of species collected over the season at a site. As most genera only included one or a few aphids, each genus was treated as a unique species in these analyses. Unidentified specimens were excluded from analyses.

All aphid specimens were categorized in three ways, according to their species or genus functional traits (Halbert et al. 2003, Verbeek et al. 2010, Boquel et al. 2011, Mello et al. 2011, Pelletier et al. 2012):

1. colonization status (binary distinction between potato colonizer or non-colonizer),
2. vector status (binary distinction between PVY vector or non-vector),
3. transmission efficiency (non-binary distinction between non-vector, undefined vector (no accepted transmission efficiency), low-transmitting vector (transmission efficiency <0.1 probability), or high-transmitting vector (transmission efficiency >0.1 probability)).

Analysis

For analyses, the sampling unit was the research site. The NY results were analyzed as follows. All functional community composition variables (proportion PVY vector species, and proportion low-transmitting, high-transmitting, and undefined vector species) were zero-inflated (a common issue with count data) and were analyzed using a hurdle model, a two-step model that first evaluates the effect of predictor variables in a binomial linear regression and then in a truncated linear regression assessing values

greater than zero. The hurdle models included two predictor variables: time period (defined below) and the percentage of agricultural land within 500 m. The results of the hurdle models dictated the type of regression model that was used to evaluate possible interaction between time period and land use. Probit models were used to evaluate response variables where there was a significant difference between zero and non-zero values, and truncated linear regression was used where there was no significant difference between the two.

Because hurdle models do not allow for an interaction term, probit or truncated generalized linear regression models were used to determine if there was an interaction between spatial and temporal predictor variables. Intra-annual variation was measured as time period (early, weeks 1–4; midseason, weeks 5–8; late, weeks 9–12; and end of season, weeks 13–15), in order to avoid temporal autocorrelation. Landscape composition was measured as agricultural intensity within 500 m of the sampling site (low, 0–25% cropland; medium, 26–50% cropland; high, 51–75% cropland; and very high, 76–100% cropland). The proportion vector species and the proportion low-transmitting species were assessed using a Poisson error distribution, as models using a binomial error distribution could not resolve the log likelihoods.

Aphid abundance and species richness were not zero-inflated and were assessed using a generalized mixed-effects model, with a Poisson distribution. Because some sites were sampled in more than one year, sampling site was included as a random effect. Similarly, because the WI results were not zero-inflated, all response variables were analyzed using generalized mixed-effects linear regression model with a Poisson distribution. Because sites were not sampled in both years, the sampling site was not included as a random effect.

The average percent cropland and unmanaged land and the average number of aphids per trap of the two study regions were compared using Wilcoxon signed-rank tests. All analyses were conducted in STATA (StataCorp, College Station, Texas, USA) (SE-64, version 15) and R (version 3.2.1).

Results

Study region and aphid community comparison

The WI study region had significantly lower mean percent unmanaged land and significantly higher mean percent cropland within 500 m compared to the NY study region. The WI sites had approximately 25% greater mean percent cropland and approximately 36% less mean percent unmanaged land within 500 m than the NY sites (Table 1). The WI study region also had

Table 1. Results of Wilcoxon signed-rank tests comparing descriptive statistics between the NY and WI sampling regions.

	NY		WI		W	*P*-value
State Category	Total	Percent	Total	Percent	Comparison	
Total aphids	1606	100	4413	100		
Vector	1056	65.75	3088	69.98	0	1.00
Non-vector	550	34.25	1219	27.62	1	1.00
Colonizing	97	6.04	106	2.40	1	1.00
Non-colonizing	1509	93.96	4307	97.60	0	1.00
Unestimated vector	347	21.61	1147	32.89	0	1.00
Low-transmitting vector	537	33.44	1358	30.77	1	1.00
High-transmitting vector	172	10.71	283	6.41	1	1.00
Average aphid abundance	40.1		267.2		3.5	**4.59E−09**
Average aphid abundance per trap	1.0		1.1		221.5	**3.96E−02**
Average percent agriculture	47.9		77.9		100	**8.91E−06**
Average percent natural habitat	45.6		9.4		627	**5.81E−07**

Notes: Data included in this table are as follows: category of comparison (the response variable in the analysis), the response variable for NY, the response variable for WI, and the results of the Wilcoxon signed-rank test. Where presented, percentages were used as the response variable. Bold *p*-values are statistically significant.

significantly greater aphid abundance than the NY region. However, this difference is unlikely to be important in practice, as the WI sites had an average of 1.14 times higher aphid abundance per trap (Table 1).

In NY, the 1606 identified aphids collected over the two seasons included 87 species and genus groups (these were used when the species could not be determined). In WI, the 4413 identified aphids included 110 species and genus groups. There was a wide range in the abundance of different species captured. In both study regions, *A. pisum*, a non-colonizing species with low PVY transmission efficiency, was the most abundant species captured overall, while the most abundant potato-colonizing species was *M. euphorbiae*.

The two study regions had similar functional aphid community compositions (Table 1). Of the 1606 identified specimens in NY, approximately 66% were PVY vectors: 22% were undefined vectors, about 33% were low-transmitting vectors, and about 11% were high-transmitting vectors. In WI, approximately 70% of the identified specimens were PVY vectors: 33% were undefined vectors, 31% were low-transmitting vectors, and 6% were high-transmitting vectors. The vast majority of specimens (approximately 94% in NY and 98% in WI) were non-colonizing species. Only approximately 6% and 2% were potato-colonizing species in NY and WI, respectively, all of which were PVY vector species (Table 1).

Prediction 1: Spatiotemporal effects will have a significant impact on the aphid community

In this study, landscape composition and intra-annual variation interacted to affect aphid abundance and species richness in both NY and WI (Table 2). In both regions, the relationship between aphid abundance and landscape composition varied throughout the growing season, showing similar shifts in the relationship over time (Figs 1A, 2A). In NY, the mean abundance decreased significantly between the early season and midseason. The mid- and late-season mean abundances are significantly lower than the early-season mean abundances for all landscape composition treatments except for the midseason high-agricultural intensity treatment (Fig. 1A). The WI data were more variable, with the mean abundances decreasing throughout the season in the high- and very high-agricultural intensity treatments and increasing significantly in the medium-agricultural intensity treatment before falling again (Fig. 2A).

The interaction of landscape composition and intra-annual variation also had a significant effect on aphid species richness in both study regions (Table 2; Figs 1B, 2B). Shifts in the relationship between landscape composition and aphid species richness were similar between the two regions and similar to those for aphid abundance. The major exception was that the mean species richness in the medium landscape composition treatment in WI—unlike abundance—decreased throughout the season (Fig. 2B).

Prediction 2: Spatiotemporal effects will impact aphid functional community composition

In NY, the interaction of intra-annual variation and landscape composition significantly affected aphid functional community composition (Table 3, Figs 3, 4). The hurdle model analyses indicated that there were significant differences between the zero and non-zero treatments with respect to the proportion of aphids that were PVY vector species, the proportion that were low-transmitting vectors, and the proportion that were high-transmitting vectors (Appendix S1: Table S3). The probit models of these response variables show that they were all significantly affected by the interaction of intra-annual variation and landscape composition. However, although there are some clear numerical differences, there are few significant differences. The proportion of aphids that were vector species and the proportion that were high-transmitting vector species were quite variable, fluctuating over the course of the season (Figs 3A, 4B). In both cases, only the late-season medium-agricultural intensity treatment was significantly different from the baseline treatment (early-season low-intensity treatment).

The proportion of low-transmitting vector species showed a clear numerical trend, decreasing throughout the growing season in all landscape composition treatments (Fig. 4A). However, only the late-season medium- and high-intensity agriculture were significantly different from the baseline treatment (early-season low-intensity treatment).

Hurdle model analysis found that there was no significant difference between treatments

Table 2. Results of generalized linear mixed models (NY data) and generalized linear models (WI data) with Poisson distribution assessing the interactive effect of time and landscape treatments on aphid abundance and species richness.

Model	Time treatment	Landscape treatment	Coef	SE	*z*	*P*-value	95% CI	95% CI
NY aphid abundance	Early	Medium	−0.502	0.444	−1.13	0.259	−1.373	0.369
	Early	High	−0.035	0.441	−0.08	0.936	−0.900	0.829
	Early	Very high	−1.786	0.548	−3.26	**0.001**	−2.861	−0.711
	Midseason	Low	−1.391	0.134	−10.37	**0.000**	−1.653	−1.128
	Midseason	Medium	−1.308	0.445	−2.94	**0.003**	−2.180	−0.436
	Midseason	High	−0.239	0.439	−0.54	0.587	−1.099	0.622
	Midseason	Very high	−3.197	0.654	−4.89	**0.000**	−4.479	−1.914
	Late	Low	−1.533	0.174	−8.81	**0.000**	−1.874	−1.192
	Late	Medium	−2.812	0.47	−5.98	**0.000**	−3.733	−1.892
	Late	High	−1.059	0.445	−2.38	**0.017**	−1.932	−0.186
	Late	Very high	−4.567	0.800	−5.71	**0.000**	−6.135	−2.998
NY species richness	Early	Medium	−0.248	0.234	−1.06	0.289	−0.706	0.210
	Early	High	−0.158	0.241	−0.66	0.511	−0.631	0.314
	Early	Very high	0.362	0.329	−1.1	0.271	−1.006	0.282
	Midseason	Low	−0.888	0.159	5.58	**0.000**	−1.200	−0.576
	Midseason	Medium	−0.908	0.235	−3.87	**0.000**	−1.368	−0.448
	Midseason	High	−0.288	0.23	−1.25	0.211	−0.739	0.163
	Midseason	Very high	−1.372	0.492	−2.79	**0.005**	−2.336	−0.409
	Late	Low	−1.216	0.226	5.37	**0.000**	−1.659	−0.772
	Late	Medium	−2.085	0.286	−7.28	**0.000**	−2.646	−1.524
	Late	High	−1.248	0.252	−4.95	**0.000**	−1.742	−0.754
	Late	Very high	−2.983	0.771	−3.87	**0.000**	−4.493	−1.472
WI aphid abundance	Early	High	1.224	0.103	11.94	**0.000**	1.023	1.425
	Early	Very high	0.946	0.095	9.95	**0.000**	0.760	1.133
	Midseason	Medium	0.676	0.112	6.03	**0.000**	0.457	0.896
	Midseason	High	−0.027	0.123	−0.22	0.826	−0.269	0.214
	Midseason	Very high	0.449	0.096	4.66	**0.000**	0.260	0.638
	Late	Medium	0.135	0.134	1.00	0.315	−0.128	0.398
	Late	High	−0.777	0.151	−5.14	**0.000**	−1.073	−0.480
	Late	Very high	0.146	0.990	1.47	0.141	−0.048	0.339
	End	Medium	(empty)					
	End	High	−0.762	0.237	−3.22	**0.001**	−1.226	−0.299
	End	Very high	−0.164	0.124	−1.32	0.187	−0.408	0.080
WI species richness	Early	High	0.533	0.145	3.66	**0.000**	0.248	0.818
	Early	Very high	0.458	0.126	3.64	**0.000**	0.211	0.704
	Midseason	Medium	−2.1E−16	0.167	0.00	1.000	−0.327	0.327
	Midseason	High	−0.034	0.159	−0.21	0.831	−0.346	0.278
	Midseason	Very high	0.071	0.127	0.55	0.579	−0.179	0.320
	Late	Medium	−0.275	0.196	−1.41	0.159	−0.659	0.108
	Late	High	−0.671	0.189	−3.56	**0.000**	−1.041	−0.301
	Late	Very high	−0.28	0.133	−2.11	**0.034**	−0.540	−0.021
	End	Medium	(empty)					
	End	High	−0.588	0.284	−2.07	**0.038**	−1.144	−0.032
	End	Very high	−0.238	0.163	−1.46	0.145	−0.559	0.082

Note: Bold *p*-values are statistically significant.

with zero and non-zero values for the proportion of undefined vectors species (Appendix S1: Table S3). The proportion of aphids that were undefined increased throughout the season. The midseason low- and high-intensity agriculture treatments and the late-season low-, medium-, and high-intensity treatments had a significantly greater proportion of undefined vector species compared to the baseline treatment (early-season low-intensity treatment; Table 3, Fig. 3B).

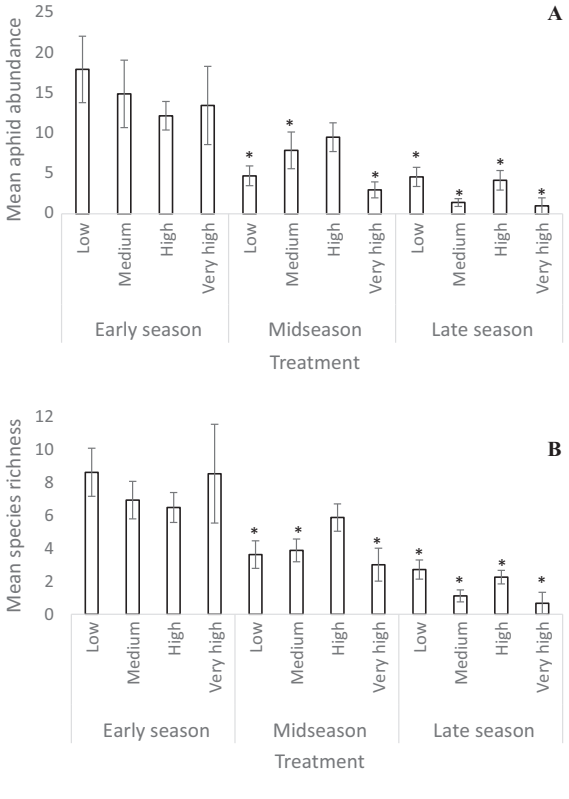

Fig. 1. The (A) average aphid abundance and (B) species richness in each time treatment (early season, weeks 1–4; midseason, weeks 5–8; and late season, weeks 9–12; and end of season, weeks 13–15) and landscape composition treatment, measured as agricultural intensity within 500 m of the sampling site (low, 0–25% cropland; medium, 26–50% cropland; high, 51–75% cropland; and very high, 76–100% cropland) in NY. Asterisks indicate significant difference from the early-season low-intensity treatment.

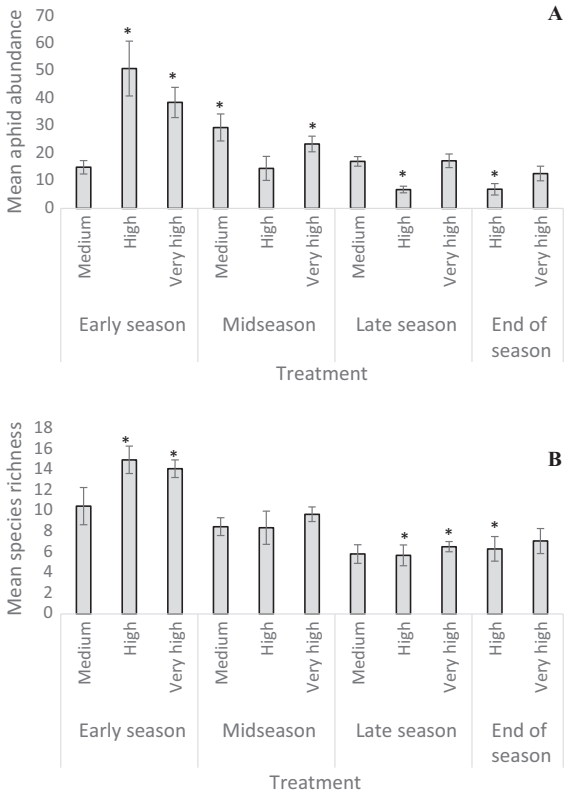

Fig. 2. (A) The average aphid abundance and (B) species richness in each time treatment (early season, weeks 1–4; midseason, weeks 5–8; and late season, weeks 9–12; and end of season, weeks 13–15) and landscape composition treatment, measured as agricultural intensity within 500 m of the sampling site (low, 0–25% cropland; medium, 26–50% cropland; high, 51–75% cropland; and very high, 76–100% cropland) in WI. Asterisks indicate significant difference from the early-season low-intensity treatment.

In WI, spatiotemporal effects had no effect on aphid functional community composition (Appendix S1: Table S4).

Discussion

Overall, there was high species diversity among aphid alates trapped, including over 60 species in each year. Despite significant differences in the surrounding landscape composition of the two study regions, several of the most abundant species in the WI study region, such as *A. pisum* and *C. eleagni*, were also among the most abundant in NY. In both regions, over 90% of specimens were non-colonizers of potato, and over 66% were known PVY vectors. The interaction of landscape composition and intra-annual variation affected aphid abundance and species richness in both study regions, and functional community composition in NY. Our results indicate that landscape composition and seasonal variation interactively shape the aphid community in both diversified and simple cropping systems.

Prediction 1: Spatiotemporal effects will have a significant impact on the aphid community

The interaction of landscape composition and intra-annual variation had a significant effect on

Table 3. Results of truncated and probit regression models of the interactive effect of landscape composition (percent cropland) and intra-annual variation on the proportion of aphids that were vectors, and the proportion that were low-transmitting, high-transmitting, and undefined vectors in NY.

Model	Time treatment	Landscape treatment	Coef	SE	*z*	*P*-value	95% CI	95% CI
Proportion of aphids that were undefined vector species (truncated regression)	Early	Medium	−0.119	0.255	−0.47	0.642	−0.619	0.381
	Early	High	−0.120	0.255	−0.47	0.639	−0.620	0.381
	Early	Very high	−0.597	0.685	−0.87	0.384	−1.939	0.746
	Midseason	Low	0.436	0.210	2.07	**0.038**	0.024	0.848
	Midseason	Medium	0.284	0.197	1.44	0.15	−0.103	0.671
	Midseason	High	0.456	0.198	2.31	**0.021**	0.068	0.843
	Midseason	Very high	(empty)					
	Late	Low	0.765	0.209	3.65	**0**	0.355	1.175
	Late	Medium	0.667	0.212	3.15	**0.002**	0.252	1.083
	Late	High	0.772	0.199	3.88	**0**	0.382	1.162
	Late	Very high	0.403	0.358	1.13	0.259	−0.298	1.104
Proportion of aphids that were low-transmitting vector species (probit Poisson regression)	Early	Medium	−0.013	0.379	−0.03	0.972	−0.756	0.730
	Early	High	0.087	0.410	0.21	0.832	−0.716	0.890
	Early	Very high	−0.201	0.651	−0.31	0.758	−1.477	1.076
	Midseason	Low	−0.409	0.403	−1.02	0.31	−1.199	0.380
	Midseason	Medium	−0.452	0.372	−1.21	0.225	−1.182	0.277
	Midseason	High	−0.318	0.383	−0.83	0.405	−1.069	0.432
	Midseason	Very high	−0.606	1.044	−0.58	0.562	−2.653	1.441
	Late	Low	−0.270	0.484	−0.56	0.577	−1.217	0.678
	Late	Medium	−1.379	0.508	−2.72	**0.007**	−2.374	−0.385
	Late	High	−1.299	0.483	−2.69	**0.007**	−2.247	−0.352
	Late	Very high	−13.517	519.323	−0.03	0.979	−1031.372	1004.338
Proportion of aphids that were high-transmitting vector species (probit binomial regression)	Early	Medium	0.134	0.289	0.46	0.644	−0.432	0.699
	Early	High	−0.417	0.427	−0.97	0.33	−1.254	0.421
	Early	Very high	0.251	0.378	0.66	0.506	−0.489	0.992
	Midseason	Low	−0.651	0.399	−1.63	0.103	−1.432	0.131
	Midseason	Medium	−0.480	0.330	−1.45	0.146	−1.126	0.167
	Midseason	High	−0.192	0.315	−0.61	0.543	−0.810	0.426
	Midseason	Very high	−0.154	0.748	−0.21	0.837	−1.620	1.312
	Late	Low	−1.764	0.980	−1.8	0.072	−3.683	0.156
	Late	Medium	−2.719	1.010	−2.69	**0.007**	−4.700	−0.739
	Late	High	−0.714	0.386	−1.85	0.064	−1.470	0.042
	Late	Very high	(empty)					
Proportion of aphids that were PVY vector species (probit Poisson regression)	Early	Medium	0.087	0.372	0.23	0.815	−0.642	0.816
	Early	High	0.087	0.410	0.21	0.832	−0.716	0.890
	Early	Very high	−0.201	0.651	−0.31	0.758	−1.477	1.076
	Midseason	Low	−0.215	0.387	−0.56	0.578	−0.974	0.543
	Midseason	Medium	−0.278	0.362	−0.77	0.443	−0.987	0.432
	Midseason	High	−0.031	0.364	−0.08	0.933	−0.744	0.683
	Midseason	Very high	−0.606	1.044	−0.58	0.562	−2.653	1.441
	Late	Low	−0.136	0.465	−0.29	0.770	−1.047	0.775
	Late	Medium	−1.092	0.465	−2.35	**0.019**	−2.002	−0.181
	Late	High	−0.412	0.387	−1.06	0.287	−1.170	0.346
	Late	Very high	−1.012	1.044	−0.97	0.333	−3.059	1.036

Notes: These models were selected based on the results of hurdle models. Bold *p*-values are statistically significant.

aphid abundance and species richness in both study regions. Overall, aphid abundance and species richness decreased through the season in both study regions. The decrease in aphid abundance over time could be explained by climatic variables, with higher temperatures and lower precipitation, either directly (by decreasing aphid fitness or movement) or indirectly (by

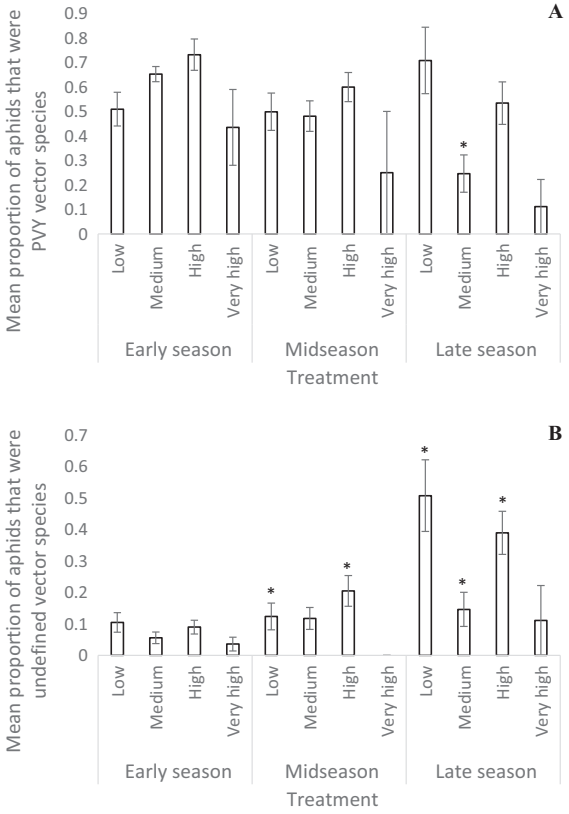

Fig. 3. The average proportion of aphids that were (A) PVY vector species (probit Poisson model) and (B) undefined PVY vector species (truncated regression model) in each time treatment (early season, weeks 1–4; midseason, weeks 5–8; and late season, weeks 9–12; and end of season, weeks 13–15) and landscape composition treatment, measured as agricultural intensity within 500 m of the sampling site (low, 0–25% cropland; medium, 26–50% cropland; high, 51–75% cropland; and very high, 76–100% cropland) in NY. Asterisks indicate significant difference from the early-season low-intensity treatment.

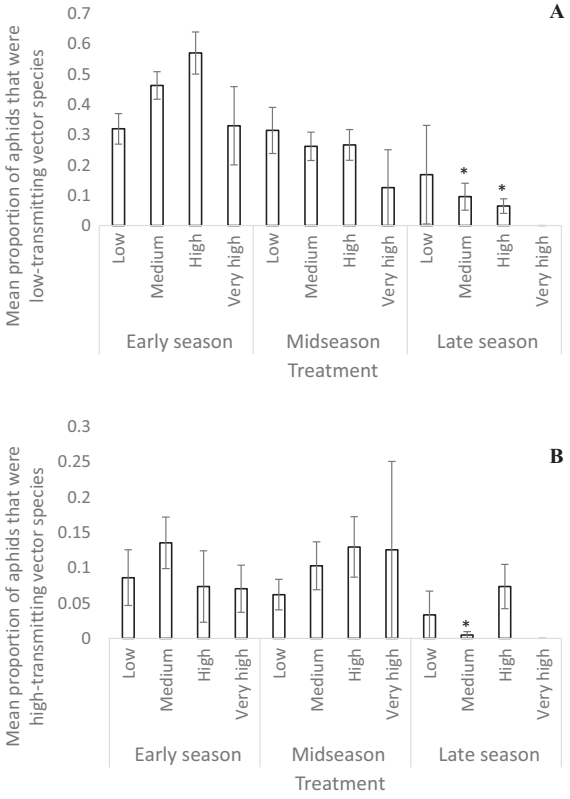

Fig. 4. The average proportion of aphids that were A) low-transmitting PVY vector species (probit Poisson model) and B) high-transmitting (probit binomial model) PVY vector species in each time treatment (early season, weeks 1–4; midseason, weeks 5–8; and late seasons, weeks 9–12; and end of season, weeks 13–15) and landscape composition treatment, measured as agricultural intensity within 500 m of the sampling site (low, 0–25% cropland; medium, 26–50% cropland; high, 51–75% cropland; and very high, 76–100% cropland) in NY. Asterisks indicate significant difference from the early-season low-intensity treatment.

decreasing host plant or ant mutualist fitness) reducing aphid abundance as the season progresses (Adler et al. 2007, Barton and Ives 2014). Ma et al. (2015) found that increasing the number of extreme high-temperature events changed the aphid community structure, with species-specific responses to increased temperature driving the shift. Management strategies, such as greater irrigation or harvesting, may also reduce aphid abundance through the season (Matis et al. 2008). Krauss et al. (2011) found that aphid abundance was significantly greater in conventional fields compared to organic and that conventional fields that sprayed insecticides had higher late-season aphid abundance than those that did not. It is unsurprising that aphid species richness followed a similar pattern to aphid abundance. Aphid abundance and species richness are often strongly correlated, and the same factors driving one could influence the other.

Prediction 2: Spatiotemporal effects will impact aphid functional community composition

The differences in effect between WI and NY suggest that there may be significant differences in the drivers of aphid functional community composition between regions and that the relationship between spatiotemporal factors and the aphid community is more nuanced than predicted. The interactive effect of landscape composition and intra-annual variation was only significant effect in NY. This may be due to the fact that the NY study region was significantly less agriculturally intense and more diverse than the WI study region. This may be an example of Tscharntke and coauthor's intermediate landscape-complexity hypothesis (Tscharntke et al. 2012), which posits that the landscape-moderated effectiveness of local conservation efforts will be highest in simplified landscapes compared to cleared or complex landscapes. Therefore, temporal and land use differences within 500 m may have a more pronounced effect on the aphid community in regions that are not so intensively farmed. These results may also reflect species differences in physiology, life history (e.g., Rothamsted Insect Survey), and differences in management practices between the two regions. Aphid abundance often exhibits species-specific responses to landscape complexity and climate (Banks 1998, Braschler et al. 2003, Grez et al. 2008, Zhao et al. 2015). Management practices, such as more intense insecticide use, may also significantly influence the aphid community. These practices likely differed substantially between the diversified NY study region and the agriculturally intense WI study region.

The interactive effect of landscape composition and intra-annual variation on the NY aphid community has implications for aphid community composition and PVY prevalence. The fluctuating effect on the proportion of aphids that were vector species obscures differences between vector groups. Overall, the proportion of undefined vectors increased over the course of the season, and the proportion of low- and high-transmitting vectors (both colonizing and non-colonizing) decreased. This has significant management implications: As time progressed, the risk of PVY transmission becomes more difficult to estimate, as the transmission efficiencies of the vector species have not been quantified. These results also support the findings of DiFonzo et al. (1997) who found that non-colonizing aphid species, which typically have lower or undefined transmission efficiencies, have the greatest abundance. Our findings suggest that the abundance of undefined vector species may be driving late-season PVY spread in NY. These results emphasize the importance of further studies assessing the transmission efficiencies of a greater number of species, as well as evaluating vectors with different capacities separately.

Prediction 3: Sites surrounded by greater amounts of cropland will have higher proportions of efficient PVY vectors in the aphid community throughout the season

Our results suggest that the percent cropland did not have a significant effect on the proportion of efficient vectors. Landscape composition had no effect in the WI study region, and in NY, the same general trend held for all landscape treatments: The proportion of high-transmitting vectors decreased over the course of the season. This suggests that this facet of aphid community composition does not drive higher PVY prevalence at more agriculturally intense research sites.

Conclusions

Our previous work in NY shows that at these sites, greater amounts of agricultural land lead to higher final PVY prevalence, and that this effect is likely mediated by the effect of the landscape on the aphid community (Claflin et al. 2016). The results of the present study agree with the landscape-moderated concentration and dilution hypothesis (Tscharntke et al. 2012); spatiotemporal effects influence the functional traits present in local aphid communities. This work suggests that changes in the landscape shape the aphid community over time and emphasize the importance of non-colonizing species and species spillover in determining aphid community structure.

In this study, we analyzed the relationship of landscape composition, intra-annual variation (sampling week), and their interaction on local aphid communities in two regions: an agriculturally intense region in WI, and the more diverse Finger Lakes region of NY. We found a significant interactive effect of landscape composition and intra-annual variation on aphid abundance

and species richness in both study regions, and on functional community composition in NY. Our work shows that intra-annual variation, in interaction with landscape composition, is an important driver of local aphid communities and that spatiotemporal shifts in agroecosystems have significant implications for aphid functional community composition.

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